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THE PARASITIC BEHAVIOR OF
DASISTOMA MACROPHYLLA¹

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The first and perhaps only reference to the parasitic behavior of *Dasistoma macrophylla* (Nutt.) Raf. appears to be that of Pennell (1928), who in the course of his primarily taxonomic studies of the Scrophulariaceae observed parasitic attachments to buckeye, *Aesculus glabra* Willd., in Indiana. In the same paper he lists *Dasistoma* as one of the genera which may be restricted to a single host. That he had probably not learned of additional hosts in the years shortly after this observation is indicated by the fact that he stated simply that *Dasistoma* "is parasitic upon the roots of *Aesculus*" (Pennell, 1935, p. 405).

Further information on this point has been recently received from Professor Edgar T. Wherry of the University of Pennsylvania who relates an incident when Pennell noted disagreement in the ranges of *Dasistoma* and *Aesculus*

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glabra in Indiana, he communicated with C. C. Deam, saying that he felt further study would show that *Aesculus* was present wherever *Dasistoma* was. After further consideration of the range of *Aesculus* in that state, Deam agreed that this was true. Thus, it would appear that Pennell felt this species was an obligate parasite on *Aesculus*. A parallel situation has been carried in the literature for many years with regard to the host specificity of *Buckleya distichophylla* Torr., which is claimed to be restricted to hemlock, *Tsuga* (e.g., see Fernald, 1950). Such (presumed) highly specialized host-parasite relationships are to be doubted when one considers that all other chlorophyllous parasites² of the Scrophulariaceae and Santalaceae that have been studied in some detail are known to parasitize a number of hosts.

The present study was made to determine if *Dasistoma* does in fact parasitize other plants as well, thereby making it possible (if it is an obligate parasite) for it to grow in areas where *Aesculus* is absent. Further, within the Scrophulariaceae, observations on parasitism are lacking for the tribe Buchneriae, to which *Dasistoma* belongs, except for some species of *Gerardia* L. (*Agalinis* Raf.). Most previous observations are for the members of the Euphrasiae. None of the several manuals consulted (e.g., Fernald, 1950; Gleason, 1952) which cover the range of this species have included the fact that this relatively little known plant is parasitic.

As Pennell (1928, 1935) has indicated, there have been long-term differences of opinion and confusion concerning the placement of this species as to genus. It was given the name *Dasistoma (aurea)* by Rafinesque (1819), who later (1837) apparently gave it a new name *Dasistema (auriculata)*. Bentham (1846) altered the spelling to *Dasystema*, but misidentified Rafinesque's description, applying the name not to this plant but to *Aureolaria* Raf. Nuttall (1818) placed it in his genus *Seymeria*, where it has been maintained in some recent works (e.g., Fernald, 1950). I have

²Such photosynthetic parasites which obtain only a portion of their total nutrition from hosts are often referred to as semi-, half-, or partial parasites. Present knowledge concerning the role of parasitism in the life of such plants indicates that although they may persist for a limited time without hosts, parasitism is necessary for optimum development and sexual reproduction.

followed Pennell who treated it as a monotypic genus, *Dasistoma*.

Dasistoma macrophylla is a robust, yellow-flowered herb becoming 1-2 m. tall, and bearing large, dissected or pinnatifid lower leaves and narrower upper leaves which are merely toothed. Although it is described as an annual (Pennell, 1928; Gleason, 1952), the plants studied appeared to be biennial, or perhaps even perennial. Its roots are much larger than those I have examined for any of the truly annual parasitic Scrophulariaceae. Young, rosette-forming plants were found in the autumn that would presumably develop into flowering individuals the following summer, as I have noted for the related *Aureolaria pedicularia* (L.) Raf. The common name bestowed upon *Dasistoma*, mullein-foxtail (Fernald, 1950), is probably less well known and certainly more confusing than the scientific name.

This species is limited to the central states, ranging from northwestern Georgia to northeastern Texas, north to eastern Nebraska, southern Wisconsin, and northern Ohio. The observations discussed here were made in October, 1959 in Mercer County, Kentucky, 5 miles northeast of Shakertown near U. S. Route 68, in hilly, conifer-hardwood woodland over limestone. The associated species apparent at that season were *Juniperus virginiana* L., *Ostrya virginiana* (Mill.) K. Koch, *Quercus* cf. *muehlenbergii* Engelm., *Q. rubra* L., *Carya* sp., *Ulmus americana* L., *Celtis tenuifolia* Nutt., *Cercis canadensis* L., *Acer saccharum* Marsh., *Fraxinus quadrangulata* Michx., *Panicum* sp., and *Aster shortii* Lindl.

Parasitic connections were detected to the roots of two species: American elm (*Ulmus americana*) and sugar maple (*Acer saccharum*), with additional connections to what was probably a third, unidentified, woody host. Since numerous haustoria are formed by a single plant, simultaneous connections to two or more different hosts is the rule (Figs. A and C). Self-parasitic connections to the roots of the same or other individuals of *Dasistoma* were almost as frequent as those to foreign roots. In addition to their surprisingly high frequency (other root parasites have far fewer), some of the self-parasitic connections were unusual in that they lacked a distinct haustorium, the connection being suggestive

of simple root grafting. Perhaps further observations will determine whether such occurrences, which may be of considerable ecological significance, are common in such plants.

The root system of *Dasistoma* resembles that of many parasitic Scrophulariaceae in that it is whitish or light tan when fresh, but will blacken quickly upon drying. The usu-

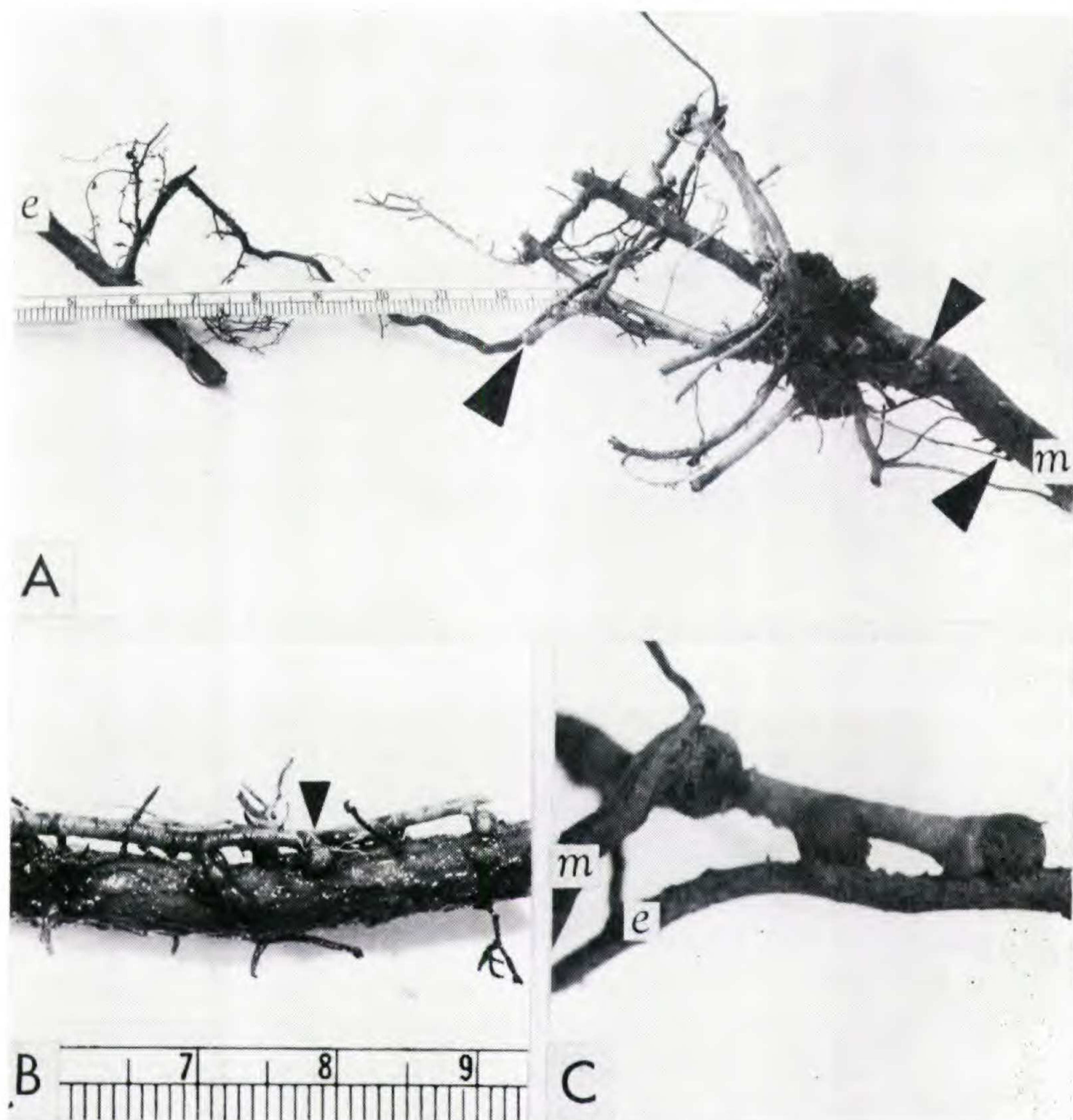


Plate 1272

Figures A-C. Parasitic connections of *Dasistoma macrophylla*. A. Haustoria of a single plant on roots of American elm (e) and sugar maple (m). Both large and relatively small haustoria are visible at the right on maple (pointers); near the center, three haustoria produced in rather close succession on elm are indicated. At the right the crown and large roots of the parasite are concentrated about roots of maple. B. *Dasistoma* root (above) paralleling a maple root to which primarily single haustoria have attached (pointer). Another haustorium is visible at the extreme right (parasite root has been severed just beyond). C. Haustoria of a single *Dasistoma* root attached both to elm and maple roots. Distal to the point of attachment, a marked decrease in the diameter of the maple root is visible, $\times 2.5$

ally disc-like haustoria, which are commonly hemispherical in vertical outline and from circular to broadly oblong in surface view, ranged from 0.5-6.0 mm. in width.

Dasistoma haustoria differ rather markedly from those of such members of the Euphrasiae as *Melampyrum lineare* Desr. (Piehl, 1962) and *Pedicularis canadensis* L. (Piehl, in press) in the following ways. They are larger on the average and lack the epidermal hairs found on some haustoria of these species. Also, they are produced from large as well as fine roots, and more frequently form attachments to larger (diameters up to 7 cm.) host organs. The larger haustoria-bearing roots, particularly, remain intact during excavation, making the observation of connections considerably easier. Another distinctive feature involving an abrupt decrease in the diameter of maple roots distal to the haustorium was noted occasionally (Fig. C); in an extreme case the development of the distal portion of roots 2.5 mm. in diameter had been arrested completely so that the host root appeared to terminate at the haustorium. The crown and large roots of *Dasistoma* differ from the above Euphrasiae in being concentrated near rather large host roots (Fig. A), the parasite roots sometimes tending to partly surround them in a manner which has its most extreme expression (in temperate North America) in certain non-green parasites, e.g., *Epifagus*. The haustoria tend to simulate those of the Euphrasiae in the mode of attachment to and penetration of host organs, and also in being produced both singly and in close succession.

It is the author's opinion that further study would show that a number of other species, the majority of them woody, serve as hosts as well. It remains to be determined if herbaceous plants also act as hosts, and if so, whether the parasite would grow as well if restricted to such plants as grasses, a situation which would involve smaller, but perhaps more numerous haustoria. — SANTA BARBARA BOTANIC GARDEN, SANTA BARBARA, CALIFORNIA.

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HETEROMORPHIC POLLEN GRAINS IN POLYMNIA¹

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During the course of a biosystematic study of the genus *Polymnia*, it was discovered that one population (Wells 254) of *P. laevigata* Beadle contained an extremely high percentage of different pollen shapes and sizes. This collection was taken from a population 5 miles southeast of Monteagle, Tennessee on U. S. Route 41. The plant was transplanted to the greenhouse and all pollen samples were taken from the living plant. This station was made known from previous collections of Ford and Russell for the University of Tennessee in 1946. Flowering heads were preserved in 3 parts 95% ethyl alcohol and 1 part acetic acid. The immature pollen was stained with aceto-carmin and studied for overall shape and number of nuclei. Aniline blue in lactophenol was used to study stainability of the mature pollen grains. Voucher slides are on deposit at The Ohio State University.

RESULTS

From observation of several hundred pollen grains, five morphological types were easily discerned as follows:

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